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Female mating competition alters female mating preferences in common gobies

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Abstract

Mating decisions can be affected by intrasexual competition and sensitive to operational sex-ratio (OSR) changes in the population. Conceptually, it is assumed that both male and female mate-competition may interfere with female reproductive decisions. Experimentally, however, the focus has been on the effect of male competition on mate choice. In many species with paternal care as in the common goby *Pomatoschistus microps*, the OSR is often female-biased and female mate-competition for access to available nesting males occurs. Using the same protocol for 3 experiments testing the effect of a perceived risk of female mate-competition, I studied female preferences for nest-holding males differing in its nest size (large/small), body size (large/small), and nest status (with/without eggs already in nest) and measured mating decisions, spawning latencies, and clutch size. Regardless of the social context, females preferred males with larger nests. A preference for large males was only expressed in presence of additional females. For nest status, there was a tendency for females to prefer mating with males with an empty nest. Here, female–female competition increased the propensity to mate. The results of this study show that females are sensitive to a female competitive social environment and suggest that in choice situations, females respond to the social context mainly by mating decisions *per se* rather than by adjusting the clutch size or spawning latency. Females base their mating decisions not only on a male's nest size but also on male size as an additional cue of mate quality in the presence of additional females.

Key words: audience effect, intrasexual competition, mate sampling, parental care, *Pomatoschistus microps*, sex-roles, size.

Studies of sexual selection have traditionally been focusing on female choice or male–male competition (Andersson 1994; Clutton-Brock and Huchard 2013), or far less frequently their interaction (Kangas and Lindström 2001; Lehtonen and Lindström 2009, reviewed in Wong and Candolin 2005). Berglund et al. (2005) emphasize that instead of splitting into the dichotomy of mate choice and intrasexual competition, there is rather a combination of both. However, most recent studies are still concentrating on either one or the other, not at potential interactions of both. The opposite phenomena, male choice and female–female competition, have been less frequently studied (Andersson 1994; Rosvall 2011; Clutton-Brock and Huchard 2013; Kvarnemo and Simmons 2013; Clutton-Brock 2017). Specifically, the interaction between female–female competition and its effects on female mating preferences and sexual selection has received very little attention, even though its importance has been acknowledged (Jennions and Petrie 1997; Cotton et al. 2006; Rosvall 2011; Rubenstein 2012; Kvarnemo and Simmons 2013).

In particular, species with male parental care (Owens et al. 1994; Almada et al. 1995; Kvarnemo et al. 1995; Borg et al. 2002; Forsgren et al. 2004), or significant male nutritional investment in the eggs (Gwynne and Simmons 1990; Simmons and Kvarnemo 2006) often show female–female competition for access to male parental investment. In such cases, parental investment defined as "any investment by the parent in an individual offspring that

increases the offspring's survival and reproductive success at the cost of the parent's ability to invest in other current or future offspring" (Smiseth et al. 2012) may differ little between the 2 sexes. Consequently, sex-roles, defined by which sex has the higher parental investment and is thus limiting the reproduction of the other sex (Trivers 1972; Kokko and Jennions 2008), can rapidly change in response to the availability of the opposite sex in the mating pool, expressed as the operational sex-ratio (OSR) (Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996; Borg et al. 2002; Forsgren et al. 2004; Simmons and Kvarnemo 2006). Thus, female–female competition should occur when access to males or breeding resources such as nest sites limits reproduction.

In gobies, males exclusively provide parental care in their nests to which females add their eggs. Those nests are maintained and defended by territorial males. Males may simultaneously accommodate clutches of several females in their nests (Miller 1984). While most species with paternal care are assumed to follow the general scheme of choosy females, male courtship displays and male–male competition (Andersson 1994), some gobies stick out from that well-known picture: female courtship behavior occurs and males may be choosy (Magnhagen 1998; Borg et al. 2002; Forsgren et al. 2004), the OSR fluctuates and is often female-biased (Borg et al. 2002, 2006; Forsgren et al. 2004; Mück and Heubel 2018), and strength and direction of sexual selection may shift (Wacker et al. 2013, 2014). Furthermore, in some gobiid species, also females are colorful (Takahashi 2000; Amundsen and Forsgren 2001; Massironi et al. 2005; Svensson et al. 2009). Especially in the small and short-lived common goby *Pomatoschistus microps*, both males and females mate repeatedly during a single reproductive season (Miller 1975). However, males can only accommodate a relatively small number of egg clutches in their nests (Magnhagen and Vestergaard 1993; Pampoulie et al. 2001; Mück and Heubel 2018). Hence, in this system, I expect female–female competition to play an important role despite non-reversed sex-roles, that is, higher potential reproductive rates (PRR) in males than in females and higher costs of reproduction in females and hence still females limiting reproduction in this species (Clutton-Brock and Vincent 1991; Ahnesjö et al. 2008). Results from an earlier study on reproduction under different OSRs and competitive environments in common gobies show that females suffer from intrasexual competition and adjust their reproductive decisions to compensate for reduced future chances of reproductive success (Heubel et al. 2008). Female–female competition can be expected to affect not only reproductive effort, but also female mate choice behavior (Heubel et al. 2008; Hayes et al. 2016).

For gobies, studied in standard mate choice trials with a choosing focal female and 2 simultaneous male stimuli, there is a general preference for larger, heavier, and better-conditioned males (Borg et al. 2006; Lehtonen et al. 2007; Kalb et al. 2016) and males with elevated levels of fanning, paternal care, and courtship activity (Lindström et al. 2006; Amorim et al. 2013). However, opposite or fluctuating patterns of mating preferences may exist (Svensson and Forsgren 2003; Borg et al. 2006; Lehtonen et al. 2010; Lehtonen 2012; Locatello et al. 2016). Females also prefer larger and more elaborate nests (Lindström 1992; Jones and Reynolds 1999; Lehtonen et al. 2007; Kalb et al. 2016). In addition, previous studies found that in many species with male parental care, females prefer to lay eggs in nests that already contain eggs (Kraak and Groothuis 1994; Jamieson 1995; Forsgren et al. 1996a; Requena and Machado 2015). However, it is still not well understood why such preferences exist and how they change in a competitive environment (Lehtonen and Lindström 2009; Lindström and Lehtonen 2013) or otherwise challenging environment or social context (forced mating versus free mate choice: Lindström and Kangas 1996; supply of oxygen: Reynolds and Jones 1999; filial cannibalism and female body size: Andrén and Kvarnemo 2014; reviewed: Qvarnström 2001; Wong and Candolin 2005).

It is widely acknowledged that mating decisions are affected by intrasexual competition for access to gametes or resources required for mating (Andersson 1994; Wong and Candolin 2005; Ahnesjö et al. 2008; Candolin and Wong 2008; Brooks and Griffith 2010) or presence of an audience (Plath et al. 2008; Ziege et al. 2009). Therefore, underlying preferences may be constrained by intrasexual interactions, which may range from simple detection probability or reduced mate assessment opportunities to contest competition and hence involvement in aggressive interactions, overridden choices, or switch to alternative mating tactics, leading to variation in the extent and direction of sexual selection. However, it is usually tested with a focus on males, for example, male–male competition compromising the ability of females to evaluate mates (Kangas and Lindström 2001; Lehtonen and Lindström 2009; reviewed in Wong and Candolin 2005). The current experiments will contribute to understanding the effect of female competition on female preferences. This is especially relevant as in nature for many fish species with male parental care, a female-biased OSR is common, and hence females often compete for access to nesting males (Borg et al. 2002; Forsgren et al. 2004; Mück and Heubel 2018).

The aim of this study is to test the effect of a perceived risk of female–female competition on female mate choice decisions. Thus, I will conduct female mate choice trials with binary choices for stimuli of varying quality: (1) male size (large versus small), (2) males with different nest sizes (large versus small), and (3) males with different nest status (already with versus without eggs) in female-competitive compared with non-competitive situations, imposed by the presence or absence of audience females. As female mating decisions may be expressed in various ways, I measured the propensity of mating, the mating decision, the latency until spawning, and the clutch size.

Under competitive situations, females can respond by being less choosy and more likely to make compromised, suboptimal but faster decisions with regard to mate and nest attributes and hence compromising quality for lower costs of mate choice given a perceived threat of limited future mating opportunities. Given this scenario, I would expect females to show no preferences, shorter spawning latencies, and unadjusted clutch sizes. Alternatively, females may exhibit preferences for specific or additional cues, adopt choosy mate sampling strategies, and hence rather adjust mating decisions to increase the benefits of their current mating decision by carefully basing their mate choice on further cues relevant under the current circumstances. The latter would rather lead to lower mating propensities, stronger preferences, longer spawning latencies, and adjusted clutch sizes. Thus, female competition may either commence, reinforce, or weaken female preferences for males with larger nests, larger body size, and nests that already contain eggs.

Materials and Methods

Experimental paradigm

In binary choice tests with or without additional audience females in an adjacent compartment, I tested the effect of female–female competition on female mate choice preferences for nest size (large versus small), male size (large versus small), and nest status (with or without eggs) in an annual benthic fish with paternal care.

Study species

The common goby is a small short-lived marine fish with male parental care. On shallow soft bottoms, males build and defend nests under mussel shells or other hard structures by excavating a cavity in the sand and gathering sand on top of the shell (Nyman 1953). Eggs are deposited on the ceiling in a single layer of these burrows and receive paternal care until hatching through fanning and protection from predators (Vestergaard 1976). Natural nest availability, nest substrates, and nest characteristics vary greatly across the Baltic Sea (Nyman 1953; Magnhagen and Vestergaard 1991; Forsgren et al. 1996b; Mück and Heubel 2018). Males can receive several egg clutches of different females, depending on the size of the nest, and care for all eggs simultaneously during a single breeding cycle (Magnhagen and Vestergaard 1993). Competition for mussel shells and other nest structures can be fierce (Borg et al. 2002; Mück and Heubel 2018) and large males often manage to obtain larger shells, which can also result in more eggs in their nest (Magnhagen and Vestergaard 1993). The OSR and the extent of female–female competition varies spatially and temporally (Borg et al. 2002; Mück and Heubel 2018), rendering the common goby a good model to study the effect of perceived risk of female–female competition on female mating preferences for direct and extended male phenotypes.

Fish collection and housing

All behavioral experiments were conducted during the major part of the common goby breeding season in June and July in the northern Baltic Sea at Tvärminne Zoological Station, Finland. Fish were collected from the field in the Tvärminne Archipelago by hand trawling in Sandvik, a bay at Henriksberg (latitude 59.83 N, longitude 23.14 E) near the station. For at least 3 and up to 10 days post-catching fish were maintained in large (size 70 cm × 50 cm or 80 cm × 80 cm), sex-separated stock tanks. Each tank had a 2–4 cm sand layer and a continuous flow-through of brackish sea water. Water quality, light conditions, and temperature followed natural conditions. Non-transparent sides of tank prevented interaction between tanks. Fish were fed once a day *ad libitum* with frozen chironomid larvae with supplementary feeding with live mysids *Neomysis integer*, and uneaten food was removed. After the experiment, fish were released back into their natural habitat.

General procedures

Before the experiment, I measured total body length (to the nearest 1 mm) and wet body weight (to the nearest 0.001 g) in all individuals. To be able to track male nest ownership and identity, all males were individually marked with 2 color marks (injected subcutaneously on the dorsal surface of the body to the left and the right of the dorsal fin) using visible implant elastomer tags (Northwest Marine Technology, USA).

Experimental tanks were divided into 3 partitions with 2 clear removable, tightly fitted dividers with small holes for water flow between sections. Some of the tanks also had a clear permanent divider with small holes to provide an additional long rear compartment to hold the additional audience females providing a perception of a female-competitive environment (Figure 1A). To prevent male–male interactions, the 2 opposing outer sections were used for the 2 stimulus males, both equipped with a halved flowerpot as a nesting resource (Lehtonen and Lindström 2009). Each pot had a removable piece of a transparent plastic sheet fit on the inside onto which females attached their eggs in a single layer when spawning (Lindström 2001; Vallon et al. 2016).

After measuring and tagging, males were transferred to their individual sections in experimental tanks. Experimental tanks were (without additional rear compartment) 70 cm × 25 cm or (equipped with a parallel divider to offer an additional rear 15 cm wide compartment for audience females along the long side of the tank) 60 – 70 × 40 cm (Figure 1A).

Study design

Using the same general experimental framework of always having half of the experimental tanks either with or without 6 additional females in the adjacent compartment as a perceived risk of female competition at a naturally realistic level for the tested population (personal observation), I tested female mating preferences for males differing in nest size (experiment 1), male size (experiment 2), and nest status (experiment 3) (Figure 1B). To control for potential side biases, I alternated the assignment of the 2 alternative stimulus types between the left and the right end of the tank across both treatments in all 3 experiments. As response variables, I measured female mating propensity, mating decision, the latency until spawning, and the clutch size.

Experimental procedure

Both males had time to build nests overnight in the assigned male compartment at either end of the tank, which refrains males from interacting with each other during the phase of setting up territories and nest building (Lehtonen et al. 2007; Lehtonen and Lindström 2009). If one or both males did not build nests within 24 h, it was replaced by a similarly sized male. Once both males had erected their territories, I introduced the 6 additional females into the rear compartment in tanks assigned to the female competition treatment and let them acclimatize for 24 h with visual contact to the 2 males. The 6 audience females were chosen randomly from a stock tank. To insure that the audience was perceived by the test female as competitors imposing a threat for female mate-competition and challenging the access to mates rather than just as bystanders, the group of female competitors always contained at least 1 female that was larger than the focal female and at least 2 females ready to spawn as indicated by roundness.

Then a single ready-to-spawn female was introduced into the central section for overnight acclimation. The female was able to visually inspect both males and—in the female competition treatment—the audience females in the rear compartment.

The mating trial started by lifting the clear dividers that prevented the focal female from accessing the 2 males. Trials were only started when both males and the focal female and at least 3 of the audience females were visible and active.

The female and the 2 males were allowed to interact freely. However, territorial males stayed usually closely attached to their nests at the 2 opposite ends of the tank interacting with the females but only rarely with the other male. I regularly checked nest ownership and status (Kalb et al. 2016). If no mating occurred within 6 h, I checked again late in the evening and re-checked in the morning. Replicates without spawning occurred by the next morning were considered as a decision not to mate and replicates with inactive, buried males or focal females were dismissed. After 24 h, I terminated the trial and recorded the nest ownership and nest status, and the presence of eggs in their nests. Clutches were removed and photographed for egg counts.

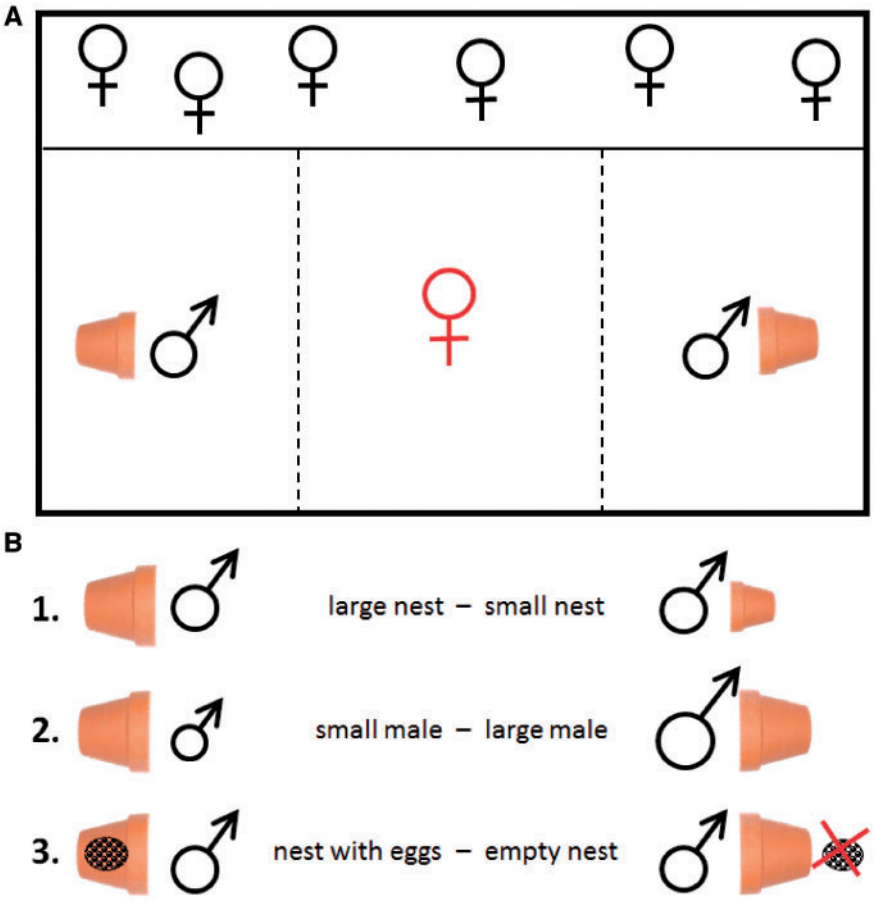

Figure 1. (**A**) The setup of experimental tanks. Depicted is the design including additional audience females in the adjacent compartment. For all experimental runs, half of the tanks were with or without female competitors, respectively. Removable dividers are drawn as dashed lines. After an acclimation period, the female had free access to both nests and males. (**B**) The design of the experiment. Females chose between nests (1) and males (2) that were either small or large (indicated by differently sized symbols, respectively). In Experiment 3, females chose between males with nests that either had eggs or where eggs had been removed.

Experiments

In the nest-size experiment (1), the female had to choose between males with large (halved flowerpots 4.5 cm ø, 4 cm depth) and small nests (3.5 cm ø, 3 cm depth). The large artificial nest represents the size of large natural nests in the local population (Mück and Heubel 2018) and fits 2–3 clutches (personal observation). The small artificial nest represents the average size of nests in the local population and fits about 1–2 clutches (Mück and Heubel 2018). Males were size matched ($n = 80$, size difference 0.5 ± 0.05 mm, mean ± SE).

In the male-size experiment (2), I tested female mating preferences for a large versus a small male while nests were size-matched (halved flowerpots 4.5 cm ø, 4 cm depth). The size difference between the 2 males was at least 3 mm ($n = 100$, 5.1 ± 0.15 mm) (mean ± SE). This size difference is equivalent to the standard deviation of the mean male size for males with observed mating success in the studied population (unpublished data).

In the nest-status experiment (3), I offered the choice between males with nests that already contain eggs versus without eggs. Males and nests (4.5 cm ø) were size-matched. The males started with identical initial conditions in terms of mating status: both males had already mated with another female the previous day. I removed the initial female egg donors and randomly replaced 1 males' clutch by a clean piece of transparent plastic.

Data handling and statistical analysis

Females always had the option not to spawn at all within the experimental time frame given the set of offered potential mates. Therefore, I tested the propensity to mate, specifically, whether the probabilities for spawning to take place differed between the social contexts. For all other analyses on mating decisions given the 2 offered alternative stimuli, trials with spawnings in both nests (3 cases) and trials without any spawning were excluded. For cases with clear signs of filial cannibalism, that is, residues of mucus but no eggs in places on the spawning substrate (Mück and Heubel 2018), I excluded data for clutch size. In the nest-size experiment (1), there was an initial n of 126 trials leading to a final sample size of $n = 68$ for trials in which mating took place in 1 nest ($n = 67$ for clutch size). In the male-size experiment (2), I analyzed $n = 53$ trials with data for spawning, $n = 50$ for latency, and $n = 48$ for clutch size (out of 102 trials in total). In the nest-status experiment (3) out of initially $n = 38$ trials, 31 with matings were used in the analysis. To control for any side biases, the assignment of the 2 different stimuli to either the left or right side of the aquaria was continuously alternated in both social contexts and all 3 experiments. To refute occurrence of side-biases, I tested whether the probability for spawning differed on the left and the right side. There was no difference between experiments and over all experiments spawning took place with the stimulus male on the left 72 times and on the right 58

times, $\chi^2 = 1.507$, $P = 0.2195$. Digital images of egg clutches were analyzed using Image J (Image J 1.43s public domain software Wayne Rasband, NIH, USA). Clutch size was analyzed as clutch area (mm^2) as the number of eggs is strongly linearly related to the clutch area (Heubel et al. 2008). As response variables I tested mating propensity (yes, no), mate choice (stimulus 1, stimulus 2), latency until spawning (min), and clutch size (mm^2). Binary female mating decisions were tested using nominal logistic models and log-likelihood ratio tests. Continuous response variables (latency, clutch size) were tested using linear models. I checked residual plots to confirm model assumptions. For latency data, I initially also checked whether a log transformation would improve the models. In the male-size experiment (2), 2 outliers (beyond 97.5 quantile) had to be excluded to meet model assumptions when analyzing latencies. All linear models included 2 fixed factors to represent the experimental design: the *social context* (female competition, control) and the *mating partner* (stimulus 1, stimulus 2). Using a model selection approach, I always started from an initial full model including as independent variables the 2 factors, all interactions, and female size as covariate. I then simplified models by iteratively removing interaction terms starting from the highest order terms and least significant terms. I compared models with respect to minimize the Akaike Information Criteria ($\Delta AIC > 2$) to obtain the best minimum adequate model. Non-significant ($P > 0.05$) covariates and interaction terms were only excluded from the model if removal improved the model fit. Factors included as part of the experimental design were never removed from the linear model. Statistical analyses were done using SAS JMP v. 13.0.0 (© 2016 SAS Institute Inc.) and R 3.3.1 (R Core Team 2016).

Results

Nest-size experiment (1)

More than 75% of spawnings took place in the larger nest. Irrespective of presence or absence of female competitors, females preferred to lay their eggs in the larger nest (with female competitors: $n = 25$, $\chi^2 = 9.64$, $P = 0.002$; without female competitors $n = 43$, $\chi^2 = 15.49$, $P < 0.001$; Table 1 and Figure 2A). There was no difference in the mating propensity (i.e., the proportion of the likelihood for mating to take place) between the 2 social contexts ($\chi^2 = 3.135$, $P = 0.077$; Table 1).

The latency until spawning did not differ between the 2 *social contexts* (with or without female competitors; $F_{1,65} = 0.137$, $P = 0.712$). The onset of spawning took longer in the smaller nest [latency for small nests: 733 min ± 146, for large nests: 402 ± 76 (mean ± SE); $F_{1,65} = 4.172$, $P = 0.045$]. There was no *social context*: *nest size* interaction and no effect by female body size, Figure 2B).

Clutch size was not affected by *social context* ($F_{1,63} = 1.034$, $P = 0.313$) or *nest size* ($F_{1,63} = 0.279$, $P = 0.599$). There was no *social context*: *nest size* interaction. Larger females spawned more eggs (female total length $F_{1,63} = 21.431$, $P < 0.0001$, slope estimate $\beta = 27.02 \pm 5.84$, Figure 2C).

Male-size experiment (2)

The mating propensity did not differ between the 2 social contexts ($\chi^2 = 0.067$, $P = 0.796$; Table 1). Females preferred large over small males in the competition context. With female competitors present, more than 75% of spawnings took place with the larger male ($n = 28$, $\chi^2 = 9.72$, $P = 0.002$; Table 1 and Figure 3A). Without female competitors, females had no specific male size preference ($n = 25$, $\chi^2 = 0.04$, $P = 0.841$). There was a significant effect of the *social context* treatment on whether or not females had a preference for larger males (log likelihood ratio test 2×2 table: $n = 53$, $\chi^2 = 4.21$, $P = 0.040$; Table 1 and Figure 3A).

The latency until spawning did not differ between the 2 social contexts (with or without female competitors; $F_{1,47} = 0.759$, $P = 0.376$; Figure 3B). Spawnings that took place with the larger male started sooner (367 ± 26 min) than trials in which females

Table 1. Mating propensity and mating decisions for females in presence or absence of a perceived risk of female mating competition in 3 experiments testing female preferences for males differing in nest size (1), body size (2), or nest status (3)

Setup	Treatment	Mating		χ^2	P	Stimulus choice	Stimulus 1	Stimulus 2	χ^2	P
Experiment 1: nest size		Yes	No			Nest size	Large nest	Small nest		
							n	*n*		
	Control	46	27	4.94	**0.026**	*N* = 43	34	9	15.49	**<0.001**
	Competition	25	28	0.17	0.680	*N* = 25	20	5	9.64	**0.002**
	Nest size					*N* = 68	54	14	25.12	**<0.001**
	Social effect*			3.14	0.077	*N* = 68			0.01	0.927
Experiment 2: male size		Yes	No			Male size	Large male	Small male		
	Control	25	21	0.35	0.555	*N* = 25	13	12	0.04	0.841
	Competition	29	27	0.07	0.789	*N* = 28	22	6	9.72	**0.002**
	Male size					*N* = 53	35	18	5.55	**0.018**
	Social effect*			0.07	0.796	*N* = 53			4.21	**0.040**
Experiment 3: nest status		Yes	No			Nest status	Already eggs in nest	Empty nest		
	Control	11	6	1.47	0.225	*N* = 11	4	7	0.81	0.366
	Competition	20	1	17.19	**<0.001**	*N* = 20	6	14	3.20	0.074
	Nest status					*N* = 31	10	21	3.90	**0.048**
	Social effect*			6.19	**0.013**	*N*=31			0.13	0.718

Notes: Experiment 1: size-matched males. Experiment 2: size-matched nests. Experiment 3: size-matched males and size-matched nests. Both males had eggs; in 1 randomly chosen nest earlier eggs were removed = "empty nest". *Social effect: log-likelihood ratio tests testing whether the probability of response is different across social contexts. $P < 0.05$ printed in bold.

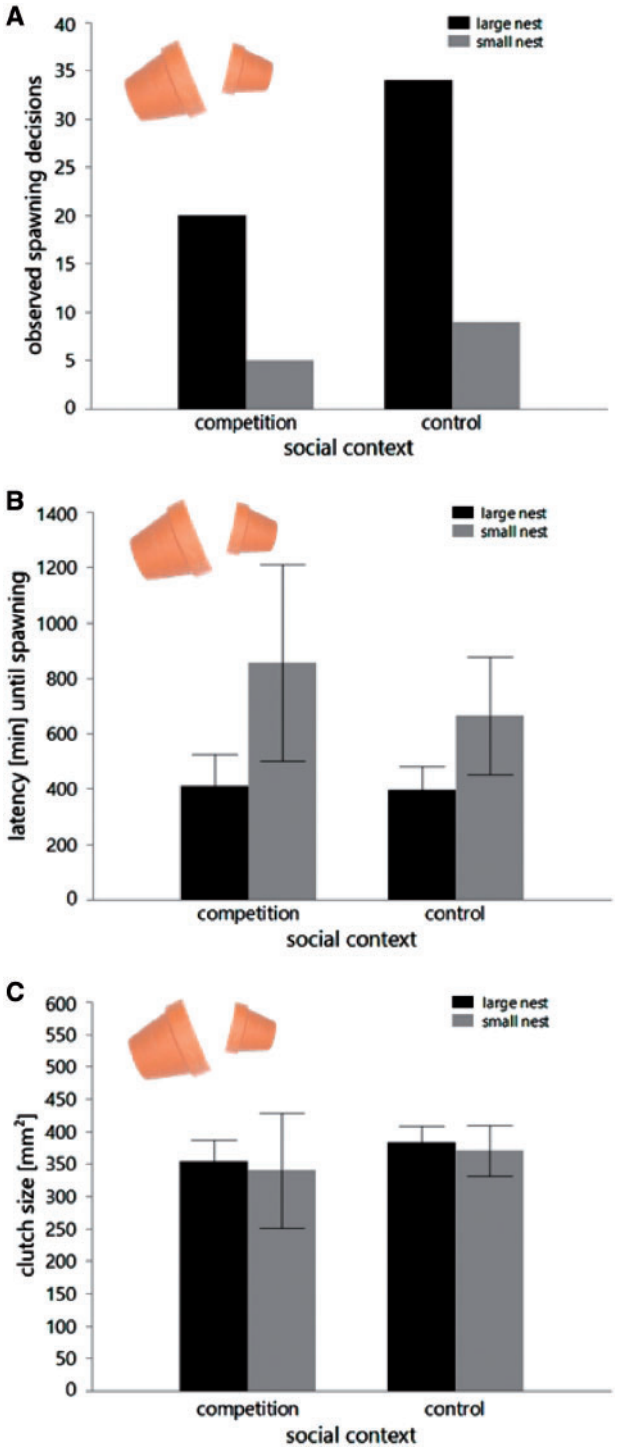

Figure 2. Nest-size experiment (1): testing female preferences for nest size. The 2 male stimuli were size-matched. (**A**) The number of observed spawning decisions as binary outcomes with males in either the larger (black) or smaller (gray) nest under the 2 different social contexts, either with or without female competitors present in the adjacent compartment. (**B**) The time in minutes (mean ± SE) until the female spawned with 1 of the 2 males (in black matings with the male in the larger nest, in gray matings with the male in the smaller nest). (**C**) The clutch area in mm^2 (mean ± SE), the female spawned with the male in the larger (black) or smaller (gray) nest in the 2 different social contexts.

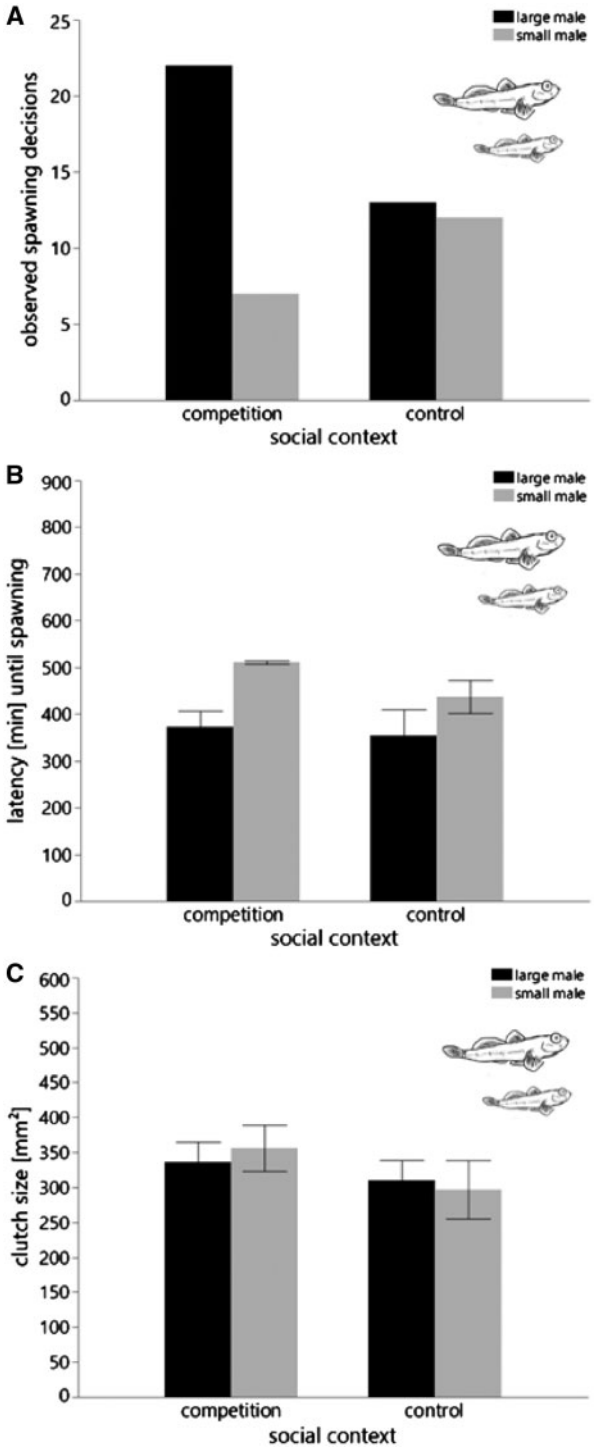

Figure 3. Male-size experiment (2): testing female preferences for male size. The 2 nests were size-matched. (**A**) The number of observed binary spawning decisions with either the larger (black) or smaller (gray) male under the 2 different social contexts, either with or without female competitors present in the adjacent compartment. (**B**) The time in minutes (mean ± SE) until the female spawned with 1 of the 2 males (in black with the larger male, in gray with the smaller male). (**C**) The clutch area in mm^2 (mean ± SE), the female spawned with the larger (black) or smaller (gray) male in the 2 different social contexts.

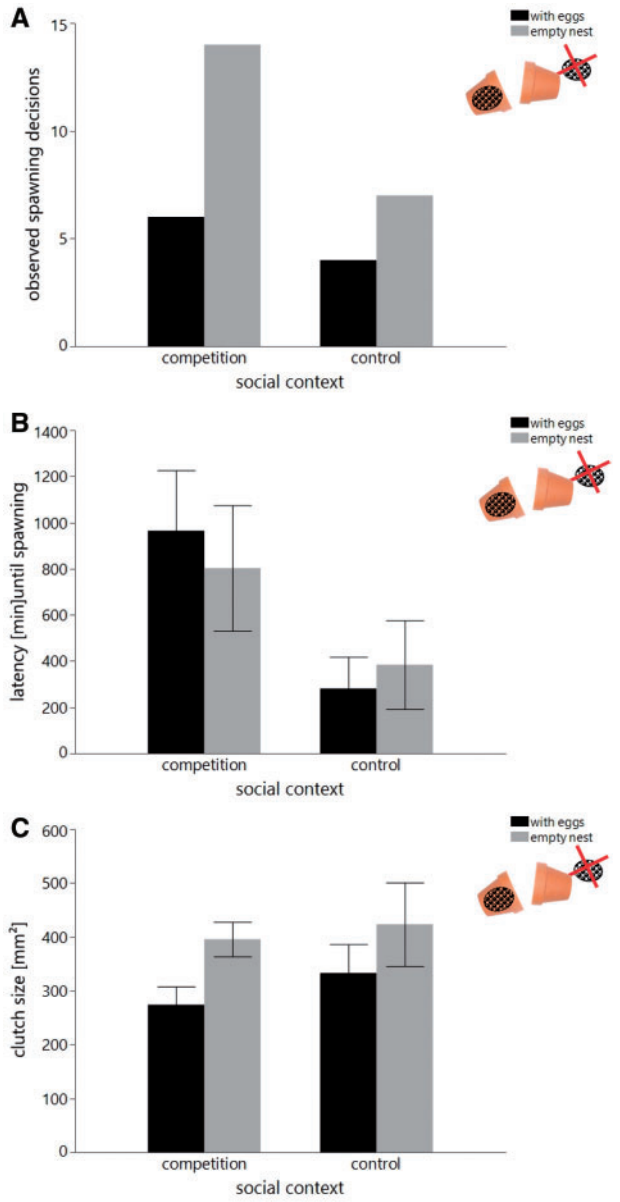

Figure 4. Nest-status experiment (3): testing female preferences for nest status. The 2 males and nests were size-matched. (**A**) The number of observed binary spawning decisions with the male in either the nest already with eggs (black) or the nest without eggs (gray) under the 2 different social contexts, either with or without female competitors present in the adjacent compartment. (**B**) The time in minutes (mean ± SE) until the female spawned with a male in 1 of the 2 nests (in black with eggs, in gray without eggs). (**C**) The clutch area in mm^2 (mean ± SE), the female spawned with the male in the egg-containing nest (black) or the nest without eggs (gray) in the 2 different social contexts.

mated with the smaller male (462 ± 35 min) ($F_{1,47} = 5.785$, $P = 0.020$). There was no *social context*: *male size* interaction and no effect by female body size (Figure 3B).

Clutch size was not affected by *social context* ($F_{1,44} = 0.033$, $P = 0.857$) or *male size* ($F_{1,44} = 0.020$, $P = 0.887$, Figure 3C). There was no *social context*: *male size* interaction. Larger females spawned more eggs (female total length as a covariate: $F_{1,44} = 26.975$, $P < 0.001$, slope estimate $\beta = 33.52 \pm 6.45$).

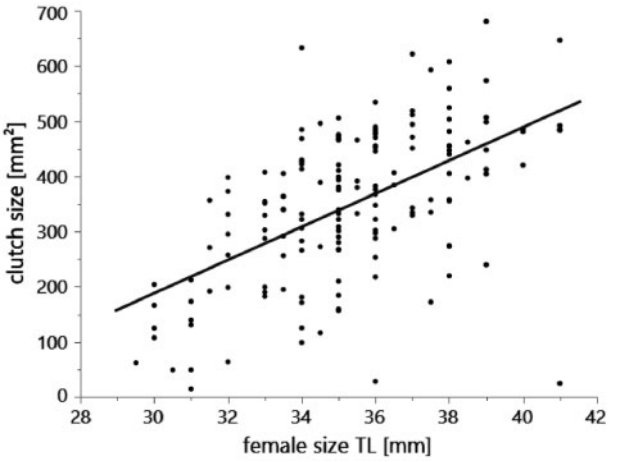

Figure 5. The relationship between clutch size (mm^2) and female total length (mm) across all 3 experiments and both social context treatment. Larger females spawned more eggs ($r^2 = 0.31$, $y = 30.07x - 713.76$).

Nest-status experiment (3)

The mating propensity differed between the 2 social contexts ($\chi^2 = 6.192$, $P = 0.013$; Table 1). There was a higher mating propensity in trials with female competitors present in the adjacent compartment (95% in the competition treatment, 69% in the control treatment; Table 1). Sixty-eight percent of all spawnings occurred in the empty nest (*nest status* effect: $n = 31$, $\chi^2 = 3.90$, $P = 0.048$). The pattern of mating decisions did not differ depending on presence or absence of female competitors (*social effect*: log-likelihood ratio test, 2× 2 table, $n = 31$, $\chi^2 = 0.13$, $P = 0.718$). Analyzing probabilities for mating with males in either empty nests or nests that already contain eggs for the 2 social contexts separately gives nonsignificant results (without female competitors 64% spawning in empty nest: $n = 11$, $\chi^2 = 0.81$, $P = 0.366$; with female competitors 70% spawning in empty nest: $n = 20$, $\chi^2 = 3.2$, $P = 0.074$; Table 1 and Figure 4A).

The latency until spawning neither differed between the 2 social contexts ($F_{1,27} = 0.029$, $P = 0.866$) nor between empty nests and those that already contained eggs ($F_{1,27} = 2.82$, $P = 0.105$). There was no *social context*: *nest size* interaction and no effect by female body size (Figure 4B).

Clutch size was not affected by *social context* ($F_{1,26} = 2.095$, $P = 0.159$) or *nest status*, that is whether nests were empty or already contained eggs ($F_{1,26} = 2.026$, $P = 0.166$; Figure 4C).There was no *social context*: *nest status* treatment interaction. Larger females spawned more eggs (female total length as a covariate: $F_{1,26} = 8.259$, $P = 0.008$, slope estimate $\beta = 31.00 \pm 10.79$).

Across all 3 experiments, larger females laid larger clutches ($r^2 = 0.31$, $F_{1,154} = 70.062$, $P < 0.001$; Figure 5). This relationship did not differ between the 3 experiments and was the same for clutches laid in presence or absence of female competitors (Figure 5). There was no relationship between male properties (size, weight, condition factor) and clutch size or spawning latency. In addition, neither spawning latency and egg number, nor male and female size were correlated.

Discussion

Females had a general spawning preference for males in larger nests. In contrast, a preference for mating with larger males only occurred under perceived female–female competition. Given a choice between

males with nests that already contain eggs and those without eggs, females rather spawn with the male in the empty nest and more so in the female-competitive context. Spawning latencies, the time it took until mating, were shorter for matings with males in larger nests and with larger males. The social context, more specifically the perceived risk of female competition, had no effect on how long it took females to start spawning in any of the 3 experiments. Clutch size only depended on female size: larger females laid larger clutches. The perceived risk of female competition did not affect how many eggs a female spawned. Interestingly, in the experiment offering females a choice between males with nests that already contain eggs versus males with empty nests, female competitors present in an adjacent compartment led to a higher mating propensity and thus a higher probability for females to decide to mate within a day.

Females prefer males with large nests

Studies on female mating preferences in the closely related sand goby *Pomatoschistus minutus* found similar preferences for larger and higher built nests (Svensson and Kvarnemo 2005; Lehtonen et al. 2007). In absence of male competition, males selected their nests size-assortatively (Kvarnemo 1995). However, not only as an indirect cue for the quality of the nest-holding male, also more directly are nests also crucial resources required for reproduction, for which females should intensively compete (Clutton-Brock 2009). Females can and should use information on nest size and quality as an indicator of indirect or direct benefits if this renders a reliable cue of quality and gained resource benefits are sufficiently grand (Kokko 1998). Indeed, larger common goby males are better at competing for large nest sites and nest maintenance and thus have more eggs in their nests than smaller males (Magnhagen and Vestergaard 1993). The observed clear preference for larger nests—both in terms of where to lay the eggs and how fast to decide whom to mate with—in the nest-size experiment (1) suggests that nest size may be a reliable and easy to evaluate indicator of mate quality in common gobies. I initially also aimed at testing female preferences for male size and nest size in mismatched and matched combinations. However, whenever I staged asymmetric trials with small males in larger nests and larger males in smaller nests, both males swapped nests prior to mating (unpublished data) hinting at potentially male–male interactions reliably solving nest selection among males prior to mating (Japoshvili et al. 2012). Lehtonen et al. (2007) used a similar setup showing a female association preferences for the larger males in the larger nests. Thus, the nest could be considered to be a part of the male's extended phenotype (Dawkins 1982; Schaedelin and Taborsky 2006). However, the relationship between male body condition and nest attributes may be unstable and thus under certain conditions, females should rather rely on multiple cues for mate choice (Candolin 2003; Lehtonen and Wong 2009).

Social context matters: females use male size as additional cue

One such additional cue may be directly assessing male size upon female mate choice decisions in situations when nests appear equally large. Interestingly, in the current study, females expressed a preference for mating with larger males only when female competitors were present. A situation with an excess of females may at the same time be perceived as a shortage of nests and mating opportunities. Hayes et al. (2016) found similar results for female fiddler crabs exhibiting stronger preferences for larger claws under female biased conditions. This pattern of an emerging preference for larger males in a female-competitive situation supports my hypothesis of more careful mate choice decisions based on additional cues. Such behavior may aim at maximizing mate quality, paternal care performance, male competitive abilities, and reproductive success in a socially challenging environment in which males are expected to conduct more demanding paternal care and nest defense duties. Larger common goby males and males in good condition are also better as intruders, by taking over other, smaller, males' nests (Nyman 1953; Magnhagen 1992; Svensson and Forsgren 2003). In addition, female–female competition may bear the risk of (too) many eggs inside nests leading to more demanding paternal care activities. Indeed, studies have shown that females prefer males that provide high levels of parental care (Forsgren 1997a; Östlund and Ahnesjö 1998; Lindström et al. 2006).

Numerous examples show that reproductive behavior as a whole can be sensitive to the number and the sex of conspecifics [Heubel et al. 2008; Aronsen et al. 2013; see Kokko and Rankin (2006) for a review]. Especially for male body size, conflicting patterns and annual fluctuations are known for female preferences in sand gobies (Forsgren 1992, 1997a; Kvarnemo et al. 1995; Lehtonen et al. 2010). As an example, females adjust their preferences according to the actual mating competition by a preference for larger males under increased male mating competition (Lehtonen and Lindström 2009). In competitive situations, larger males seem to be more likely to be able to maintain nests with many eggs. However, such context-dependent flexibility of mating preferences can go in either direction. Indeed, females do not always commence preferences for larger stimuli. In *Pomatoschistus marmoratus*, females preferred the smaller male and did not care about nest size when male–male competition was experimentally excluded (Locatello et al. 2016). In two-spotted gobies *Gobiusculus flavescens* and annual killifish (*Austrolebias reicherti*, Rivulidae), early during the reproductive season, when the OSR was still male-biased or even and female competition was weak, females preferred larger males. Later, toward the end of the season under female-biased sex ratios and stronger female-competition, females lost their size-related male preference (two-spotted goby: Borg et al. 2006; annual killifish: Passos et al. 2014). Such pattern rather supports the hypothesis of compromised low cost mating decisions targeted at securing immediate mating success (Heubel et al. 2008). Thus, the specific nature of a change in the context seems to be relevant for whether a cue may be added or dropped in mate assessment.

Females prefer to spawn with males in empty nests

In various species with paternal care, females prefer to add their eggs into nests that already contain eggs (reviewed in Forsgren et al. 1996a). Such behavior can be explained by the presence of eggs directly indicating good parenting skills (Sargent 1988; Kraak and van den Berghe 1992), dilution effects (Ridley and Rechten 1981; Unger and Sargent 1988), mate choice-copying (Dugatkin 1992; Gibson and Höglund 1992; Pruett-Jones 1992), increased hatching success with increasing brood size due to lowered filial cannibalism (Rohwer 1978), and expected higher paternal investment in larger and more valuable clutches (Coleman et al. 1985; Sargent 1988; Petersen and Marchetti 1989; Vallon and Heubel 2017). Alternatively, females may prefer males with empty nests or nests that only contain fewer eggs to avoid being the last (Andrén and Kvarnemo 2014). The last added clutch bears the highest risk of filial cannibalism (Salfert and Moodie 1985; Petersen and Marchetti 1989; Klug and Lindström 2008; Vallon and Heubel 2016). This alternative view is especially relevant for common gobies as a species with naturally limited space for eggs in their nest (Pampoulie et al. 2001; Mück and Heubel 2018) and selective filial cannibalism

targeted at the youngest, last added clutch (Vallon and Heubel 2016). Here, the nest-status experiment (3) showed a clear female preference for males with empty nests in a system where a second, added clutch would most likely be the last one of a brood for the current reproductive cycle.

Mate sampling and female investment

In an earlier study with females making mating decisions in a no-choice situation in a female-competitive environment, females spawned faster and more eggs [Heubel et al. 2008, but see also Myint et al. (2011) for the opposite pattern in another goby species, *Rhinogobius flumineus*]. In contrast, here I found clear differences in spawning latencies with respect to the choice of male traits but no difference in spawning latency or clutch size when competitors were present or absent. Spawning latency is a good proxy for a females' willingness to mate with a specific mate (Lindström and Kangas 1996). Prolonged latencies may reflect either a degree of reluctance to mate or be a sign of extended mate sampling (Lindström and Lehtonen 2013). In a field study on mate sampling in two-spotted gobies in a population with a known seasonal shift toward elevated female competition, females became less choosy and visited fewer males later during the reproductive season (Myhre et al. 2012). A similar study on sand gobies, however, showed the reversed temporal shift toward intensified mate sampling later in the season (Forsgren 1997b). Such longer mate sampling intervals may for example arise if females take more time evaluating potential mates in situations where mate choice cues reveal ambiguous messages such as the male evaluated as being of higher quality residing in the smaller nest, or the smaller male having built the more elaborate nest. In the current study, spawning latencies were longer for matings that ended up with the smaller male and with males in the smaller nest, the generally less preferred phenotype. Here, latency or mate sampling depended on male cues, not on the female competitive context. At first sight, this is surprising as Heubel et al. (2008) observed sooner matings in a female competitive situation. However, this was set up in a no-choice mesocosm situation and measured the time until any of the 3 competing females spawned first. Alternatively, and as a mutually non-exclusive explanation, longer latencies could also be interpreted as male mate choice. Longer latencies for matings with smaller males may well be a consequence of cases where the larger male refused to mate with the female and hence females ended up mating with the smaller, less preferred male. However, I then would have expected the same pattern in the nest-status experiment (3) and longer latencies in the female competitive treatment, a situation with more females potentially perceived available to the male. With the present study, I cannot conclude either way as I did not quantify behavior nor time budgets for males and females, which thus remains to be studied in the future.

Surprisingly, females did not adjust their clutch size to spawn more eggs when mating with males of the preferred stimulus type (Lehtonen and Lindström 2007). I expected larger clutches when mating with males in larger nests and with larger males, specifically in cases with shorter spawning latencies. I also expected females to spawn more eggs when mating under the perceived risk of female competition (Heubel et al. 2008). Nevertheless, larger females consistently spawned more eggs, which supports the common view that the fecundity of the female increases with female body size (Andersson 1994; Kvarnemo 1994).

In conclusion, reproductive decisions can be affected by the presence of the same sex conspecifics (Heubel et al. 2008). However, until now it was unclear whether and how females would adjust their mating preferences in a choice situation under different perceived risks of female mating competition. In nature, nest attributes and male attributes may usually be linked and appear as a hierarchical suite of easily accessible and more difficult but more reliable cues to evaluate mates. The results of this study emphasize that common goby females are sensitive to the presence of a female audience, imposing female mate-competition when choosing a mate. In addition to nest size as a generally preferred and easily assessable attribute of a male, females also rely on male body size as an additional more subtle cue for mate quality in the presence of additional females.

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